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Evolution of Near and Far Dispersal in Spatially Structured Habitats*

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Abstract

The evolutionary stability of short-distance and long-distance dispersal was investigated in a population on a landscape where there are spatial correlations in habitat types, and where the driving interaction between individuals is competition for space. This study explores how both the amount and the spatial arrangement of habitat can affect the evolution of dispersal strategies. Stochastic spatially explicit simulations were used, as well as differential equation models developed via pair approximations. The conditions under which either dispersal strategy can successfully invade the other are determined, as a function of the amount and clustering of suitable habitat and the relative costs involved in the two dispersal strategies. On landscapes where suitable habitat is fairly aggregated, short-distance dispersal is advantageous, since propagules which travel a short distance are more likely to land on suitable sites. On landscapes where suitable habitat is only slightly clustered or is unclustered, far dispersal, which reduces intraspecific competition, is advantageous. There are also relatively few types of landscapes on which the two dispersal strategies can each invade the other, and thus will coexist, and landscapes for which neither type can invade the other, and so whichever type colonizes first will persist. All of these results are observed even when there is no intrinsic difference in costs (such as production costs or mortality) between near and far dispersal. The spatial structure of the environment can facilitate coexistence between these competitors, or lead to the dominance of either dispersal strategy. Pair approximations do quite well at predicting the above results compared with simulations. Mixed dispersal strategies were also briefly investigated. In many cases, mixed dispersal has a strong advantage, since it can take advantage of contiguous patches of suitable habitat, but the occasional long-distance dispersal allows some individuals to escape competition with locally aggregated individuals and potentially colonize new sites. However, pair approximations do not accurately predict these latter results.

Introduction

Dispersal is a key element of an individual's life history (Howe and Miriti, 2000), since it determines the context within which the rest of that life history is played out. That context may include the physical environment in which a propagule lands, as well as aspects of the biotic environment such as local population synchrony (Lande et al., 1999) or the stability of predator-prey interactions (Kareiva, 1987). There are many potential costs of dispersal, such as energetic costs, increased mortality during or after dispersal, or

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uncertainty of the environmental quality of the new location. Dispersal also affects population genetic structure (Williams and Guries, 1994); these effects may be positive, such as the reduction of inbreeding (Perrin and Mazalov, 1999), or negative, such as disruption of adaptations to local conditions. Despite the potential disadvantages to dispersal, there are many possible benefits that in the end must prevail to some degree. For example, dispersal may reduce competition between siblings or between offspring and parents, or act as a bet-hedging strategy (Wiener and Tuljapurkar, 1994) in the face of environmental variability. More fundamentally, if a species never dispersed it could never grow into new areas, and could at best only maintain its population size. These ideas led to the fascinating result of Hamilton and May (1977), later generalized by Comins et al. (1980) and Cohen and Motro (1989), which states that no matter how high the cost, a significant proportion of reproductive effort should be allocated to dispersal.

Some amount of dispersal is a necessity for population survival and growth, but the question then remains, how far should propagules disperse? Great variability in dispersal distances is observed within communities (Augspurger, 1986; Clark et al., 1999), and even within species (Morse and Schmitt, 1985; Telenius and Torstensson, 1999). The prevalence of long-distance dispersal is a question of great concern, since it affects competition between individuals (Bolker and Pacala, 1999), the spread of invasive species, and population responses to global change (Clark et al., 1998, 1999; Higgins and Richardson, 1999; Cain et al., 2000). Localized dispersal may allow populations to take advantage of spatially clustered habitat, but it also leads to aggregation, interspecific competition, and reduced population density (Pacala, 1986).

Another issue of obvious concern is that of habitat loss and fragmentation, and how not only the amount of habitat but its spatial arrangement affects populations (Lande, 1987; Opdam, 1990; Andrén, 1994; Kareiva and Wennergren, 1995; Roland and Taylor, 1997; With et al., 1999; Kraft et al., 2002).

The question I investigate here is, how does habitat loss and fragmentation affect the evolution of short-distance versus long-distance dispersal? It is in many ways the same fundamental question addressed by Nee and May (1992), but with more emphasis on the spatial arrangements of both habitat and populations. The spatial arrangements of populations has been shown to affect population dynamics (Durrett and Levin, 1994; Rees et al., 1996; Durrett and Levin, 1998), as have the spatial patterns of habitat heterogeneity (Lavorel et al., 1994; Roland and Taylor, 1997). Habitat fragmentation affects the communities that persist in patches (Holt and Gaines, 1993), as well as the dispersal behavior of individuals (Waser, 1987; Peles et al., 1999).

Some have previously investigated the evolutionary stability of strategies which vary the amount of reproductive effort allocated to dispersal (Levin et al., 1984; Ludwig and Levin, 1991) or to short-distance versus long-distance dispersal strategies (Crawley and May, 1987; Harada and Iwasa, 1994; Durrett and Levin, 1998; Holmes and Wilson, 1998), while others have studied the evolution of more general dispersal strategies such as parameterized probability distributions for dispersal distance, typically by assuming some kind of relation between seed size, dispersal distances, and/or competitive ability (Geritz, 1995; Ezoe, 1998; Geritz et al., 1999; Levin and Muller-Landau, 2000). The approach used here is to consider only short-distance and long-distance dispersal strategies (henceforth referred to as "near" and "far" dispersal), but on heterogeneous landscapes with spatial correlations in habitat types as described in Hiebeler (2000). As in Crawley and May (1987) and Harada and Iwasa (1994), it would be best to think of the populations studied here as plants with seed heteromorphism (Venable, 1985; Venable et al., 1987), since passive dispersal with predetermined behaviors are used, rather than active dispersal where propagules capable of perceiving their environment seek out a suitable target site (e.g., Langellotto and Denno, 2001). The near and far dispersal strategies could also be viewed as sexual versus vegetative reproduction (Hartnett, 1990; Nishitani and Kimura, 1993).

Stochastic spatial simulations were used, as well as pair approximations (Katori and Konno, 1991; Matsuda et al., 1992; Sato et al., 1994; Tainaka, 1994; Harada et al., 1995; Hiebeler, 1997, 2000; Ives et al., 1998; Ferrière and Le Galliard, 2001), differential equation models which include some information about local spatial correlations. It is possible to analytically solve the pair approximation model for this system when only pure dispersal strategies are involved, to determine when one strategy can invade the other.

The Model

The habitat and population model used here is a patch-occupancy model on a lattice, similar to that used in Hiebeler (2000), with two key differences beyond the different dispersal strategies being investigated: first, the lattice used here is a hexagonal lattice, also sometimes called a triangular or honeycomb lattice, depending on whether one focuses on the vertices or the cells of the lattice; here, each site is a hexagon which has six adjacent neighboring sites. A hexagonal lattice was chosen rather than a rectangular lattice, because with the latter, one must decide whether or not to include interactions between diagonally adjacent sites. Also, if such interactions are included, one must then decide whether or not they should differ from interactions between directly adjacent sites, because diagonal sites are separated by a larger distance than orthogonally adjacent sites. Second, time is continuous rather than discrete. A continuous-time model was chosen because it simplifies the calculations in the pair approximations, and comparison with results here which overlap those in Hiebeler (2000) indicate that the same qualitative behavior is seen in discrete or continuous time with this type of model.

As in Hiebeler (2000), there are two habitat types: suitable (type 0) and unsuitable (type 1). The parameter p_0 describes the proportion of sites that are suitable, i.e. it describes habitat availability. The parameter q_{00} describes the spatial correlations, i.e. clustering of habitat types; it is defined as the probability that a randomly chosen neighbor of a suitable site is also suitable. Small values of q_{00} mean that the habitat is highly fragmented, while large values of q_{00} mean the habitat is highly clustered or aggregated. On a "random" (in the colloquial sense) landscape, where habitat types of sites are independent, then $p_0 = q_{00}$. Note that for simplicity, the habitat distribution in this model does not change over time. Landscapes consisting entirely of suitable habitat (i.e. $p_0 = q_{00} = 1$) will be referred to as uniform landscapes. Three landscapes with the same amount p_0 of suitable habitat but different clustering q_{00} are shown in figure 1.

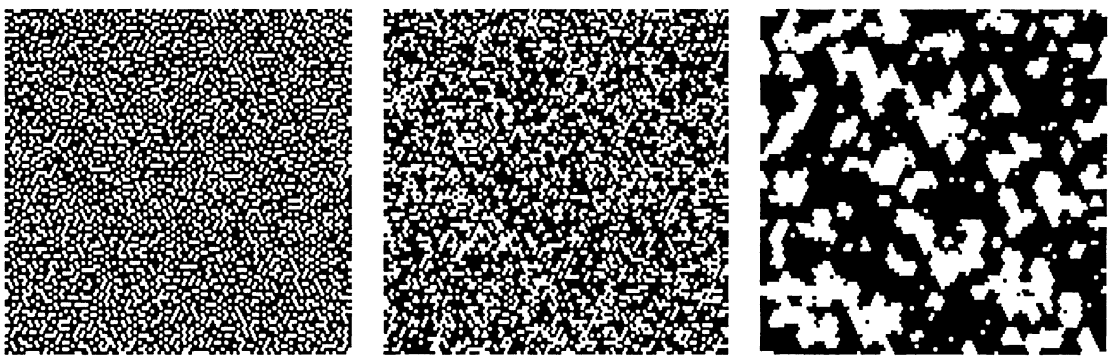

Figure 1: Three landscapes all with proportion $p_0 = 0.35$ of suitable habitat (colored white), and varying clustering parameter q_{00}. Left: $q_{00} = 0.2$ (evenly spaced habitat, or negative correlations between adjacent sites). Center: $p_0 = q_{00} = 0.35$ (no correlations between sites). Right: $q_{00} = 0.8$ (clustered habitat, or positive correlations between adjacent sites).

Using these two parameters, we can calculate the probably $p[00]$ that a 2×1 block of sites are both suitable, as $p[00] = p_0 q_{00}$. Similarly, the probability that in a block of 2 sites, the first one is suitable and the second one is unsuitable is $p[01] = p_0(1 - q_{00})$. Also, we assume rotational symmetry, so that $p[10] = p[01]$. Finally, one can compute $p[11] = 1 - p[00] - 2p[01]$. Thus, specifying $p[00]$ and $p[01]$ is an alternative equivalent way of parameterizing these landscapes. A third method would be to specify p_0, the global amount of suitable habitat, along with ρ, the correlation coefficient of habitat types among adjacent sites. In terms of the parameters used here, this correlation is

$$\rho = \frac{q_{00} - p_0}{1 - p_0}.$$

Thus on clustered landscapes where $q_{00} > p_0$ there is positive correlation between adjacent sites, and on unclustered where $q_{00} < p_0$ there is negative correlation. On random landscapes with $q_{00} = p_0$, the correlation is zero.

On these heterogeneous landscapes, we then add a patch-occupancy model. Each site in the model is in one of three states: empty suitable habitat (state 0), empty unsuitable habitat (state 1), or occupied suitable habitat (state 2). For simplicity, unsuitable habitat cannot be occupied.

Each occupied site invests energy into reproduction at a total reproductive rate of R_T, which can be applied via two types of dispersal. With "near" (short-distance) dispersal, the occupied reproducing site drops its propagule on one of the six adjacent sites, chosen at random. With "far" (long-distance) dispersal, the occupied reproducing site drops its propagule on a site chosen at random uniformly from the entire lattice. An occupied site may use a combination of dispersal strategies: proportion α of reproductive effort is allocated to far dispersal, while $1 - \alpha$ is allocated to near dispersal. Thus $\alpha = 1$ represents a pure far dispersal strategy, while $\alpha = 0$ represents pure near. Any propagules which land on an unsuitable site or an occupied site are wasted, which leads to competition for space between individuals when reproducing.

Each occupied site becomes empty at rate μ. Note that by rescaling the time variable, $\mu = 1$ could be assumed without loss of generality. See Table 1 for definitions of many of the symbols used in this study.

Note that in this model, neither type of propagule has a competitive advantage over the other. If a propagule of either type lands on an occupied site, it is wasted, no matter what type of individual is occupying that site.

Near and far dispersal each have an associated cost, c_n and c_f respectively. These costs may reflect many different factors that affect the two strategies differently, such as the cost of producing dispersal apparatus itself, total fecundity, mortality during dispersal or germination, germination ability, etc. (Morse and Schmitt, 1985). For example, if 20 small seeds which travel far can be produced using the same effort it would take to produce a single large locally-dispersing seed, then c_f would be decreased by a factor of 20 relative to c_n; if far dispersers suffer 30 times as much mortality as short-distance dispersers, then c_f would be increased by a factor of 30 relative to c_n. Competitive differences between the two types of propagules are not directly investigated here, although such competitive differences could also be included in c_n and c_f. Including the costs in calculating the rate of propagule production, near dispersal happens at rate $R_T(1-\alpha)/c_n$ per occupied site, while far dispersal happens at rate $R_T\alpha/c_f$ per occupied site. No specific relational form between the costs c_n and c_f was assumed here.

The near dispersal population thus behaves like a basic contact process in continuous time on a hexagonal lattice, with the addition of the heterogeneous habitat types (Tao et al., 1999; Hiebeler, 2000). The far dispersal population behaves like a classic metapopulation model (Levins, 1969; Hanski and Gilpin, 1991), since all sites interact equally.

To study the evolution of dispersal using the near and far dispersal modes on these landscapes, i.e. to determine which strategy was evolutionarily stable (Maynard Smith, 1982), the ability of the near disperser to invade a population of far dispersers that had reached equilibrium was determined, and vice versa. Some interactions between mixed dispersal strategies were also investigated. All of this was done via spatially explicit stochastic simulations, as well as with pair approximations. Traditional spatially implicit models or mean field approximations (e.g., Tilman, 1994) were not used, since such models cannot distinguish between near and far dispersal.

Simulations

For computational convenience, the hexagonal lattice was embedded in a rectangular lattice, where two subsets of six of the eight neighbors are used for even and odd rows (d'Humières and Lallemand, 1988). A 200×200 lattice was used for the simulations. The boundaries used here were periodic, so the lattice was actually a torus, but some exploration with truncated boundaries indicated that for a lattice of this size, the boundary type had no significant effects on the behavior of the model.

Although the model takes place in continuous time, for convenience a "step" will be defined as $40,000 =$

Table 1: Definitions of symbols.

p_0	Proportion of sites on the landscape which are suitable.
q_{00}	Clustering of suitable habitat; the conditional probability that a randomly-chosen neighbor of a suitable site is also suitable.
R_T	Total reproductive rate per occupied site.
α	Proportion of reproductive effort which is allocated to long-distance dispersal.
c_f	Cost per "near" (short-distance) propagule.
c_n	Cost per "far" (long-distance) propagule.
μ	Mortality/disturbance rate, the rate at which an occupied site becomes empty.
ϕ_n	$R_T(1-\alpha)/(6c_n)$, the rate at which an occupied site drops propagules on any particular one of its six neighboring sites via near dispersal.
ϕ_f	$R_T\alpha/c_f$, the rate at which an occupied site sends out far-dispersing propagules.
$P[ij]$	The probability that a pair of adjacent sites are in states i and j, respectively.
$Q[i\|j]$	$P[ij]/P[j]$, the probability that a randomly chosen neighbor of a state-j site is in state i.
s	$P[2]/p_0$, the proportion of suitable sites that are occupied.

200^2 events, where an event is either a "birth" (a colonization of a new site) or a "death" (an occupied site becoming empty). Thus during a step, each site in the lattice is updated on average one time, although due to the stochastic nature of the model, some sites will be updated many times or not at all.

The initial population in the simulations begins with 50% of the suitable sites occupied. From these initial conditions, the model was allowed to run for a maximum of 300 steps (i.e. 12×10^6 events). Beginning on step 100, the proportion of suitable sites occupied, s, was measured after each step. A running linear regression of s was computed over the previous 100 steps. The initial population was considered to have reached equilibrium if the slope of this regression was less than 10^{-4} and the difference between the largest and smallest values of s during the previous 100 steps was less than 0.02. These two tests ensured that the population density had settled down to an equilibrium value with only very small fluctuations.

If the initial population went extinct, the simulation was ended and no invaders were introduced. Otherwise, when the initial population had reached equilibrium or reached the maximum 300 steps, the invading population was added. Fifty sites occupied by the resident type were converted to the invading type, under the assumption that the invaders arise by mutation. One could instead add the invaders to randomly chosen suitable sites; with this model, for pure strategies, there is no difference in the results, because if either the resident or invader strategy consists of pure far dispersal, then no spatial correlations are present in that population. However, the initial distribution of the invaders may affect the success of invasion when mixed strategies are involved.

After invasion, the simulation was allowed to run for up to another 1500 steps. Beginning on step 500, separate running linear regressions were performed on the proportions of suitable sites occupied by individuals of the two different species (resident and invader) over the last 100 steps. If the slopes of both regressions were less than 10^{-4} and the spreads of s values for both species were less than 0.02, then the system was considered to have reached equilibrium. When the system reached equilibrium, reached the maximum 1500 steps, or either species went extinct, the simulation was stopped, and the final outcome recorded.

Five replicate simulations were performed (using five different landscapes), for the landscape parameters p_0 and q_{00} each ranging from 0.01 to 0.99 in steps of 0.01. Because p_0 and q_{00} must satisfy the constraint

$q_{00} \geq 2 - 1/p_0$ in order to describe feasible landscapes (Hiebeler, 2000), there are no landscapes with certain large values of p_0 and small values of q_{00}. Also, some landscapes with very small p_0 and and large q_{00} are difficult to generate via the algorithm used here, a problem which seems to be exacerbated on the hexagonal lattice; fortunately, such landscapes are not of great biological interest, as they consist of very few extremely large patches of suitable habitat surrounded by huge expanses of unsuitable sites. Because of these "missing" values of p_0 and q_{00}, simulations were only performed for approximately 5200 rather than $9801 = 99^2$ combinations of p_0 and q_{00}. Performing one set of stochastic simulations between two dispersal strategies required roughly 9 trillion pseudo-random numbers to be generated, and took approximately one week on a 933-MHz PC running Linux. Simulations were written in the C programming language for speed.

Pair approximation

Pair approximation is a technique for including local spatial correlations in a relatively simple mathematical model of a population. Pair approximation models involve a set of equations describing the configuration of 2×1 blocks (i.e. pairs) of sites, compared with the simpler and more common spatially implicit approach which only involves equations describing the behavior of single sites. Pair approximations are often simple enough to solve analytically, or solve numerically with very little effort. They allow one to study the effects of spatial correlations among populations as well as habitat types (Ives et al., 1998; Hiebeler, 2000; Ovaskainen et al., 2001), where spatially explicit simulations are very time-consuming. Earlier studies have applied pair approximations to determine the outcome of competing dispersal strategies similar to those used here (Harada and Iwasa, 1994; Durrett and Levin, 1998), but without the environmental heterogeneities.

In this model, as in Hiebeler (2000), each site may be in one of three states: 0 (empty suitable site), 1 (empty unsuitable site), or 2 (occupied suitable site). Thus the system is described by probabilities such as $P[01]$, the probability that in a randomly chosen pair of sites, the first one is empty and suitable, and the second one is unsuitable. Note that as in Hiebeler (2000), capital letters such as $P[01]$ will be used when describing probabilities involving both the habitat type and the population, while lower-case letters such as $p[01]$ will be used to denote probabilities involving only habitat types.

In general, $P[ij]$ represents the probability that in a pair of sites, the first is in state i and the second is in state j. By assumption of spatial symmetry, $P[ji] = P[ij]$. Summing over one block in a pair gives the marginal probabilities, $P[i] = \sum_j P[ij]$. Another definition which will prove useful is $Q[i|j] = P[ij]/P[j]$, the probability that a randomly chosen neighbor of a site in state j is in state i. Note that in general $Q[i|j] \neq Q[j|i]$.

Near dispersal

The three pair approximation equations for the locally ("near") dispersing population, derived in appendix A, are:

$$\frac{dP[00]}{dt} = 2P[02]\mu - P[00](10\gamma\phi_n) \quad (1)$$

$$\frac{dP[01]}{dt} = p_0(1 - q_{00})\mu - P[01](5\gamma\phi_n + \mu) \quad (2)$$

$$\frac{dP[02]}{dt} = P[00](5\gamma\phi_n - \mu) + p_0 q_{00}\mu - P[02](5\gamma\phi_n + \phi_n + 3\mu) \quad (3)$$

where $\phi_n = R_T/(6c_n)$ is the rate at which an occupied site colonizes any particular one of its six neighbors, and

$$\gamma = Q[2|0] = \frac{P[02]}{P[0]} = \frac{P[02]}{P[00] + P[01] + P[02]} = \frac{P[02]}{p_0 - P[2]} \quad (4)$$

is the conditional probability that a randomly chosen neighbor of an empty suitable site is occupied. We can define

$$s = P[2]/p_0 = (p_0 - P[0])/p_0 = 1 - (P[00] + P[01] + P[02])/p_0 \tag{5}$$

as the proportion of suitable sites that are occupied. The probability that a site is suitable and empty, i.e. in state 0, is then

$$P[0] = p_0 - P[2] = p_0(1 - s). \tag{6}$$

Stability analysis of the extinction equilibrium, derived in appendix B, shows that the equilibrium is unstable, i.e. the near-dispersing population will persist, as long as $\mu < 5\phi_n q_{00} = 5R_t/(6c_n)$ (inequality 25). In words, as long as the extinction rate μ is less than 5 times the rate of colonization per neighbor times the probability that that neighboring site is suitable, then the locally dispersing population will persist. Another intuitive interpretation is that the population will persist if a pair of adjacent occupied sites on an otherwise empty landscape will grow (Levin and Durrett, 1996). Consider one of the sites in this hypothetical pair of occupied sites on an empty lattice. It sends propagules to each of its neighboring sites at rate ϕ_n. One of those neighboring sites is occupied (because it is the other site in the occupied pair of sites), and so any propagules dropped there are wasted; each of the other five neighboring sites is suitable with probability q_{00} (and empty by assumption). So this dyad heuristic of Levin and Durrett (1996) predicts that the population will persist if the growth rate per site in the pair, $5\phi_n q_{00}$, is larger than the extinction rate μ. Inequality (25) will be modified soon to consider interaction between the two dispersal strategies; the interpretation of the equation given above will help motivate this modification.

Also note that on a uniform landscape where all sites are suitable, i.e. $p_0 = q_{00} = 1$, inequality (25) becomes $\mu < 5\phi_n$, which agrees with the results of Levin and Durrett (1996) when adjusted for the fact that my model is on a hexagonal lattice, while theirs is on a rectangular one.

Now assume that inequality (25) is satisfied, i.e. the population does not go extinct. The proportion of suitable sites that are occupied at equilibrium for the near-dispersing population, s_n^*, is derived in appendix C, and given by equation (39). Using that equation, as well as equation (6), the proportion of sites which are suitable and empty at equilibrium is

$$\begin{aligned} P_n^*[0] &= p_0(1 - s_n^*) \\ &= \frac{5p_0\left(3\phi_n - 18\phi_n q_{00} + \mu + 3\sqrt{\phi_n}\sqrt{\phi_n(6q_{00}-1)^2 + 4\mu(1-q_{00})}\right)}{30\phi_n - \mu} \end{aligned} \tag{7}$$

Also, observe that s_n^*, the proportion of suitable sites occupied at equilibrium with pure near dispersal, does not depend on p_0, the amount of suitable habitat in the landscape. For a locally dispersing population, q_{00}, the probability that a randomly chosen neighbor of a suitable site is also suitable, is the only aspect of the habitat distribution that affects the behavior of the population (Hiebeler, 2000), because q_{00} is precisely the probability that a propagule from an occupied site will land on a suitable site. The global amount of suitable habitat, p_0, doesn't matter, because the population only spreads locally. Of course, this is only really true in the limiting case of an infinitely large lattice; on finite grids with small amounts of suitable habitat, stochastic fluctuations in small populations may drive them extinct even when the model indicates they should persist.

It will also be useful to compute $Q_n^*[0|0]$ at equilibrium for the near-dispersal model. By definition, $Q^*[0|0] = P^*[00]/P^*[0] = P^*[00]/(p_0 - P^*[2])$. But using equation (36), this can be solved for

$$Q_n^*[0|0] = \frac{\mu}{5\phi_n}. \tag{8}$$

Far dispersal

The three pair approximation equations for the long-distance ("far") dispersing population, derived in appendix A, are:

$$\frac{dP[00]}{dt} = 2P[02]\mu - P[00](2P[2]\phi_f) \quad (9)$$

$$\frac{dP[01]}{dt} = p_0(1-q_{00})\mu - P[01](P[2]\phi_f + \mu) \quad (10)$$

$$\frac{dP[02]}{dt} = P[00](P[2]\phi_f - \mu) + p_0 q_{00}\mu - P[02](P[2]\phi_f + 3\mu) \quad (11)$$

where $\phi_f = R_T/c_f$ is the rate of propagule production per occupied site, and $P[2] = p_0 - P[0] = p_0 - (P[00] + P[01] + P[02])$ is the proportion of sites that are suitable and occupied.

Stability analysis of the extinction equilibrium shows that the equilibrium is unstable, i.e. the far-dispersing population will persist, as long as $\mu < \phi_f p_0 = R_T p_0/c_f$ (inequality 26). In words, as with near dispersal, this says that the long-distance dispersing population will persist as long as the extinction rate μ is less than the effective reproduction rate after accounting for those propagules which land on unsuitable sites, i.e. the reproduction rate times the probability that a site is suitable. This agrees with predictions of spatially implicit metapopulation models, since the far-dispersing population does not develop any spatial correlations, and thus behaves like a classic metapopulation model with some habitat removed.

The proportion of suitable sites that are occupied at equilibrium, s_f^*, derived in appendix C (equation 40), is

$$s_f^* = 1 - \frac{\mu}{p_0\phi_f}.$$

Note that this equilibrium doesn't depend on q_{00}, the spatial configuration of habitat on the landscape; it only depends on the amount of habitat available. This is because in the far-dispersing population, the locations and habitat types of an occupied site and the sites it attempts to colonize are independent, i.e. spatial correlations play no role.

Also using equation (40), the proportion of sites which are empty and suitable at equilibrium is

$$P_f^*[0] = p_0(1 - s_f^*) = \frac{\mu}{\phi_f}. \quad (12)$$

Interestingly, this quantity does not depend on either p_0, the amount of suitable habitat, or q_{00}, its clustering. For example as p_0 decreases, i.e. the proportion of suitable habitat decreases, the proportion of occupied suitable sites will decrease by precisely the amount needed so that the proportion of empty suitable sites remains the same. There is a simple explanation for this: at equilibrium, each site's effective fecundity (including the fact that some propagules are wasted by landing on empty or unsuitable sites) and mortality balance exactly. If we change p_0, then at the new equilibrium, effective fecundity and mortality must still be equal. Since effective fecundity is reproductive rate ϕ_f times the probability $P_f^*[0]$ that a propagule lands on an empty suitable site, then $P_f^*[0]$ must not change when we change the amount of suitable habitat, p_0. Similar reasoning explains why equation (8) does not depend on p_0 or q_{00}.

We can also calculate the frequency at equilibrium of pairs of blocks for the far-dispersing population. The actual population itself has no spatial correlations, although correlations in the habitat distribution still exist. Therefore, at equilibrium the probability $P^*[00]$ that a pair of sites are both suitable and empty is simply the probability that the two sites are both suitable, which is $p[00] = p_0 q_{00}$, times the probability that both sites are empty, which is $(1-s_f^*)^2$ because of independence of the locations of occupied sites. That is, $P_f^*[00] = p_0 q_{00}(1 - s_f^*)^2$. Using this, along with equations (6) and (40), the probability that a randomly chosen neighbor of an empty suitable site is also empty and suitable is

$$Q_f^*[0|0] = \frac{P_f^*[00]}{P_f^*[0]} = \frac{p_0 q_{00}(1-s_f^*)^2}{p_0(1-s_f^*)} = q_{00}(1-s_f^*) = \frac{q_{00}\mu}{p_0\phi_f}. \quad (13)$$

Similar reasoning leads to the following result for the probability that the neighbor of an occupied suitable site is empty and suitable:

$$Q_f^*[0|2] = \frac{P_f^*[20]}{P_f^*[2]} = \frac{p_0 q_{00} s_f^*(1-s_f^*)}{p_0 s_f^*} = q_{00}(1-s_f^*) = Q_f^*[0|0] \tag{14}$$

Mixed dispersal

The pair approximation equations for a model with mixed dispersal, derived in appendix A, are:

$$\frac{dP[00]}{dt} = 2P[02]\mu - 2P[00]\beta \tag{15}$$

$$\frac{dP[01]}{dt} = p_0(1-q_{00})\mu - P[01](\beta+\mu) \tag{16}$$

$$\frac{dP[02]}{dt} = p_0 q_{00}\mu + P[00](\beta-\mu) - P[02](\beta+\phi_n+3\mu) \tag{17}$$

where

$$\begin{aligned}\beta &= 5\phi_n Q[2|0] + \phi_f P[2] = 5\phi_n \frac{P[02]}{P[0]} + \phi_f(p_0 - P[0]) \\ &= \frac{5\phi_n P[02]}{P[00]+P[01]+P[02]} + \phi_f p_0 - \phi_f(P[00]+P[01]+P[02])\end{aligned}$$

is the total rate at which propagules land on an empty site via near dispersal from five adjacent neighbors whose states are unknown, as well as from far dispersal.

For the mixed-dispersal case, neither the stability of the extinction equilibrium nor the block probabilities at the nontrivial equilibrium can be solved for in a concise analytical form. However, they can be numerically solved using a variety of techniques discussed in appendices B and C. For the nontrivial equilibrium, once the equilibrium values $P_m^*[00]$, $P_m^*[01]$, and $P_m^*[02]$ were computed, the equilibrium values $P_m^*[0] = P_m^*[00] + P_m^*[01] + P_m^*[02]$ and $Q_m^*[0|0] = P_m^*[00]/P_m^*[0]$ were also computed for later use in determining invasibility.

Invasibility

Using pair approximations, one can consider a population with one dispersal strategy reaching equilibrium, and then being invaded by a small group of individuals with a different strategy. A full pair approximation model of one strategy reaching equilibrium and then another one invading would involve four states per site. As before, I shall let state 0 represent an empty suitable site and state 1 represent an unsuitable site. But now rather than state 2 representing an occupied suitable site, there are two types of occupied site: those occupied by the initial resident type, which I will call state a, and those occupied by the invading type, state b. Thus there are $4^2 = 16$ possible states for a pair of sites, although rotational symmetry, constraints imposed by the fixed habitat distribution, and the fact that the probabilities must sum to one reduce the number of independent variables to seven. For example, we could use $P[00]$, $P[01]$, and $P[0a]$ as before when thinking about the initial resident population, and then the additional four states $P[0b]$, $P[1b]$, $P[bb]$, and $P[ab]$ after the invader has been added.

In order to determine whether or not the invader is able to survive when invading at very low density, we should first let $P[00]$, $P[01]$, and $P[0a]$ for the resident population reach their equilibrium values. Then, holding those three probabilities constant, we can consider a four-state model using $P[0b]$, $P[1b]$, $P[bb]$, and $P[ab]$, and examine the stability of its extinction equilibrium (where all four variables are zero, in this parameterization) to determine whether or not the invader will survive. This is similar to the technique used by Takenaka et al. (1997) to study invasibility between two types of near dispersers with different fecundity/mortality ratios, only here there is the small added complexity of habitat heterogeneity.

However, there is one simplifying assumption that can be made. Rather than the full four-state model for the invader, we may simply assume that sites occupied by the resident type are in fact unsuitable, since an invader's propagule cannot colonize either type of site. Thus, we may assume $P[ab] = P[1b]$, and reduce the number of states to three. Surprisingly, comparisons of the three-state and four-state models found that this simplification gave exactly the same results during the stability analysis (although certainly the two models would diverge as the system moves away from the equilibrium, since unsuitable sites are fixed over time, while sites occupied by the resident type become empty again at rate μ). Thus, the simpler three-state model was used.

First consider a near-dispersing population, which reaches equilibrium and is then invaded by a far disperser at low density. I only consider cases where both near and far dispersers are able to survive if they are the sole population on the landscape, i.e. both inequalities (25) and (26) are satisfied.

When the resident near dispersers have reached equilibrium, the proportion of sites which are suitable and empty is given by equation (7). To the far invader, sites which are occupied by near dispersers are equivalent to unsuitable sites, i.e. both types of sites are unavailable. So to determine whether or not the far invader survives, we need only replace p_0 in equation (26) by $P_n^*[0]$ from equation (7). Thus, for far invading near, we have the following result:

Result 1 *Far dispersers can invade near dispersers if and only if*

$$\mu < P_n^*[0]\phi_f = \frac{P_n^*[0]R_T}{c_f}, \tag{18}$$

where $P_n^*[0]$ is given by equation (7).

Next, consider a far disperser, which reaches equilibrium and is then invaded by a near disperser at low density. Inequality (25) specifies the conditions necessary for a near population will survive on its own on a landscape. In that expression, q_{00} gives the probability that a near disperser's propagule will land on a suitable site. However, when near is invading far, sites occupied by the resident far type are unavailable, and therefore equivalent to unsuitable sites. Thus, q_{00} in inequality (25) should be replaced by the probability that the neighboring site is both suitable and empty. If we think of the invading near dispersers as starting out on randomly chosen empty sites, this probability is simply $Q_f^*[0|0]$ given in equation (13). If we think of the near invaders as arising by mutation from far dispersers, rather than arriving from an external source, one could argue that $Q_f^*[0|2] = P_f^*[20]/P_f^*[2]$ should be used instead, but as shown in equation (14), this has the same value as $Q_f^*[0|0]$. As usual, this is because the far-dispersing population has no spatial correlations. When $Q_f^*[0|0]$ replaces q_{00} in inequality (25), we obtain the following:

Result 2 *Near dispersers can invade far dispersers if and only if $\mu < 5\phi_n Q_f^*[0|0]$, i.e. if*

$$1 < \frac{5\phi_n q_{00}}{p_0\phi_f} = \frac{5c_f q_{00}}{6c_n p_0} = \frac{5q_{00}}{6p_0}, \tag{19}$$

the last equality assuming that $c_n = c_f$.

Finally, consider one arbitrary mixed dispersal strategy with proportion α_1 of far dispersal, which reaches equilibrium and is then invaded by a second dispersal strategy with proportion α_2 of far dispersal. Once the equilibrium values $P_m^*[0]$ and $Q_m^*[0|0]$ are computed from the first population, they may be substituted in for p_0 and q_{00} to determine the stability of the extinction equilibrium for the invading population using any of the numerical techniques described in appendix B.

Results

Consider an experiment where a second group of individuals with proportion α_2 of far dispersal tries to invade a resident population with proportion α_1 of far dispersal which has reached equilibrium. I classified the results into four possible outcomes:

1. The initial population was not able to survive on its own.
2. The initial population survived, and then the second population was unable to invade.
3. The initial population survived, the second population successfully invaded, and the two species co-existed.
4. The initial population survived, and then the second population successfully invaded and drove the first population extinct.

Only in outcomes 3 and 4 listed above do I say that the second population is able to invade the first one. (There are combinations of parameter values for which the first population alone cannot survive, but the second population can, but they are not emphasized here.)

After both complete sets of invasion experiments were performed (α_2 invading α_1, and vice versa) via simulations and pair approximations, several outcomes were possible. First, the parameter values p_0 and q_{00} for which the population went extinct were recorded, for both dispersers. These results from simulations are shown for the cases of pure near and pure far dispersal in figure 2. As predicted by equations (25) and (26) and as shown by Hiebeler (2000) on a rectangular lattice in discrete time, the survival of the near disperser essentially depends only on the habitat clustering q_{00}, and not on the amount of habitat p_0, except for very small values of p_0 when finite-size effects begin to play a role. In contrast, the long-distance disperser's ability to survive only depends on p_0, and not on q_{00}. Figure 2 shows this with surprising accuracy, because the far disperser behaves very much like a spatially implicit metapopulation, with only small stochastic fluctuations away from the predicted behavior. For comparison, the parameter values for which the populations go extinct as predicted by pair approximations are displayed in figure 3.

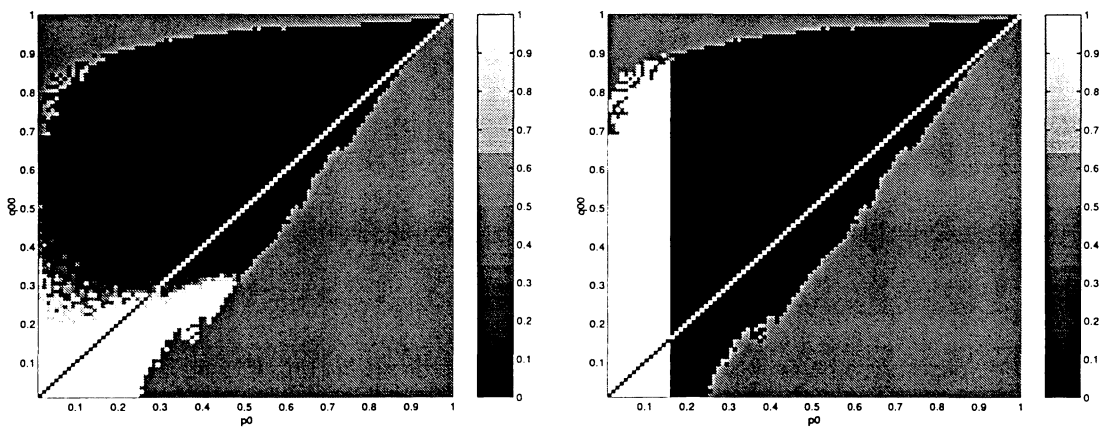

Figure 2: The proportion of times the near disperser (left) and far disperser (right) go extinct on their own, before any invasions take place, as measured from simulations. The x axis shows p_0, the proportion of sites which are suitable; the y axis shows q_{00}, the clustering of suitable habitat. The uniform gray areas in the lower-right and upper-left regions indicate combinations of p_0 and q_{00} for which landscapes are either theoretically impossible, or for which a landscape was not able to be generated. The shades of gray in the remaining areas indicate the proportion of times (out of 5 replicate simulations on independent landscapes for each combination of p_0 and q_{00}) in which the population went extinct. The near disperser goes extinct when q_{00} is small, i.e. the habitat is very fragmented. The far disperser goes extinct when p_0 is small, i.e. there is very little suitable habitat. The diagonal was highlighted to show the situation where $p_0 = q_{00}$, i.e. habitat types are independent among all sites. Parameter values (see Table 1) were $R_T = 2$, $c_n = c_f = 1$ (near and far dispersal have equal costs), and $\mu = 0.3$.

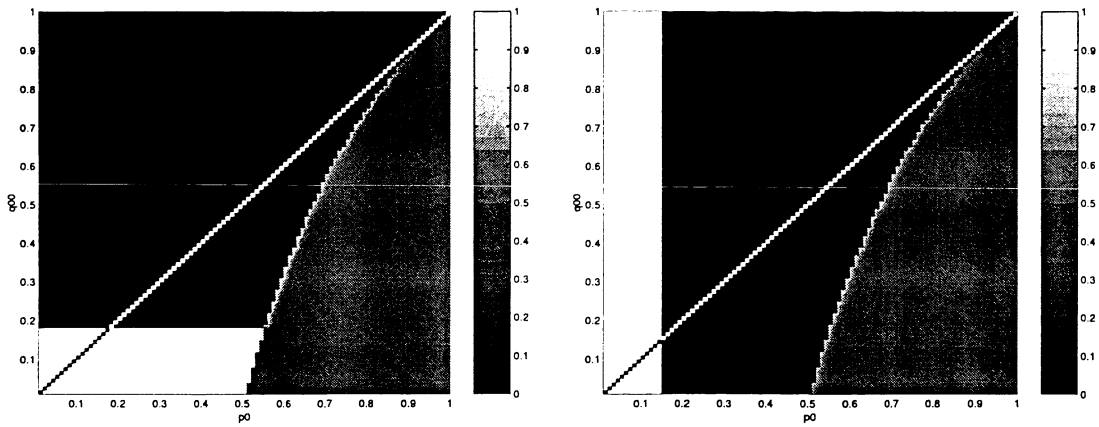

Figure 3: Parameter values for which the near disperser (left) and far disperser (right) go extinct on their own, before any invasions take place, as predicted by pair approximations. See figure 2 for further explanation, and parameter values used.

Assuming both populations are each able to survive on a landscape alone, the full invasion experiments were performed, and the results put into one of the following four categories:

1. α_1 beats α_2. This means that α_2 cannot invade α_1, and that α_1 can invade α_2. Presumably this means that α_1 will competitively exclude α_2, given enough time, since if α_2 becomes rare it will go extinct.
2. α_2 beats α_1 (analogous to the previous category).
3. Coinvasible: each strategy is able to invade the other.
4. Neither α_1 nor α_2 can invade the other.

Figure 4 shows the results for pure near and far (i.e. $\alpha_1 = 0$ and $\alpha_2 = 1$) measured from simulations, indicating which of the four categories the results fell in. Figure 5 displays the corresponding predictions from pair approximations.

Pair approximations were also computed for pure near versus pure far dispersal when the costs c_n and c_f were both varied between 0.002 and 2.5, thus varying fecundity by a factor of more than 1,000. Results are shown in figure 6.

Now consider the special case of a uniform landscape, i.e. $p_0 = q_{00} = 1$. For such a landscape, when a near disperser reaches equilibrium, equation (7) simplifies to

$$P_n^*[0] = \frac{5\mu}{30\phi_n - \mu}.$$

In order for far to invade near on a uniform landscape, equation (18) then becomes $\mu < 5\mu\phi_f/(30\phi_n - \mu)$. Assuming the near disperser is able to survive alone on the lattice, we know from equation (25) that $\mu < 5\phi_n < 30\phi_n$, thus the denominator in the condition above is positive and will not change the direction of the inequality when multiplied through. This inequality can be rewritten to give:

Result 3 *On a uniform landscape with $p_0 = q_{00} = 1$, a pure far disperser is able to invade a pure near disperser if*

$$\mu > 5R_T\left(\frac{1}{c_n} - \frac{1}{c_f}\right).$$

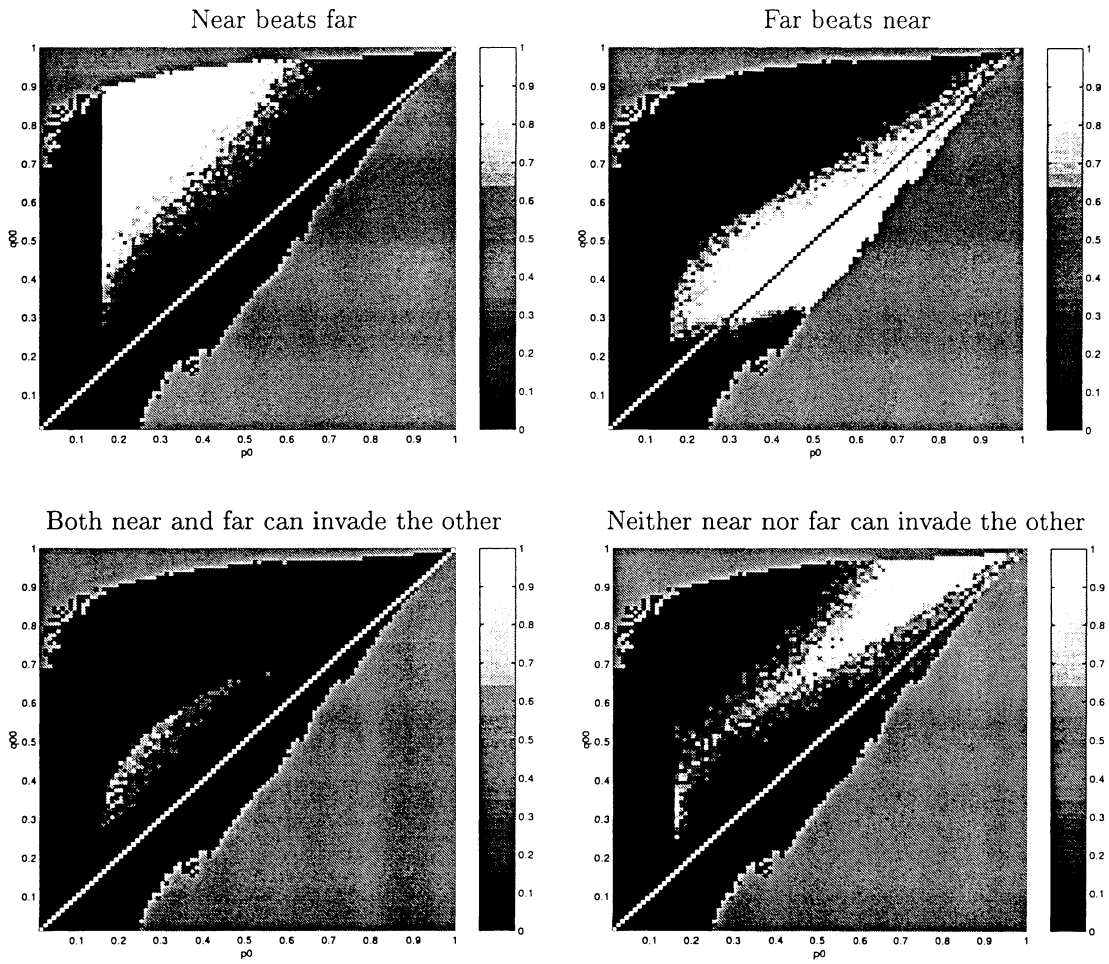

Figure 4: The four main outcomes of the invasion experiments, as measured from simulations. See text and figure 2 for further explanation, and parameter values used.

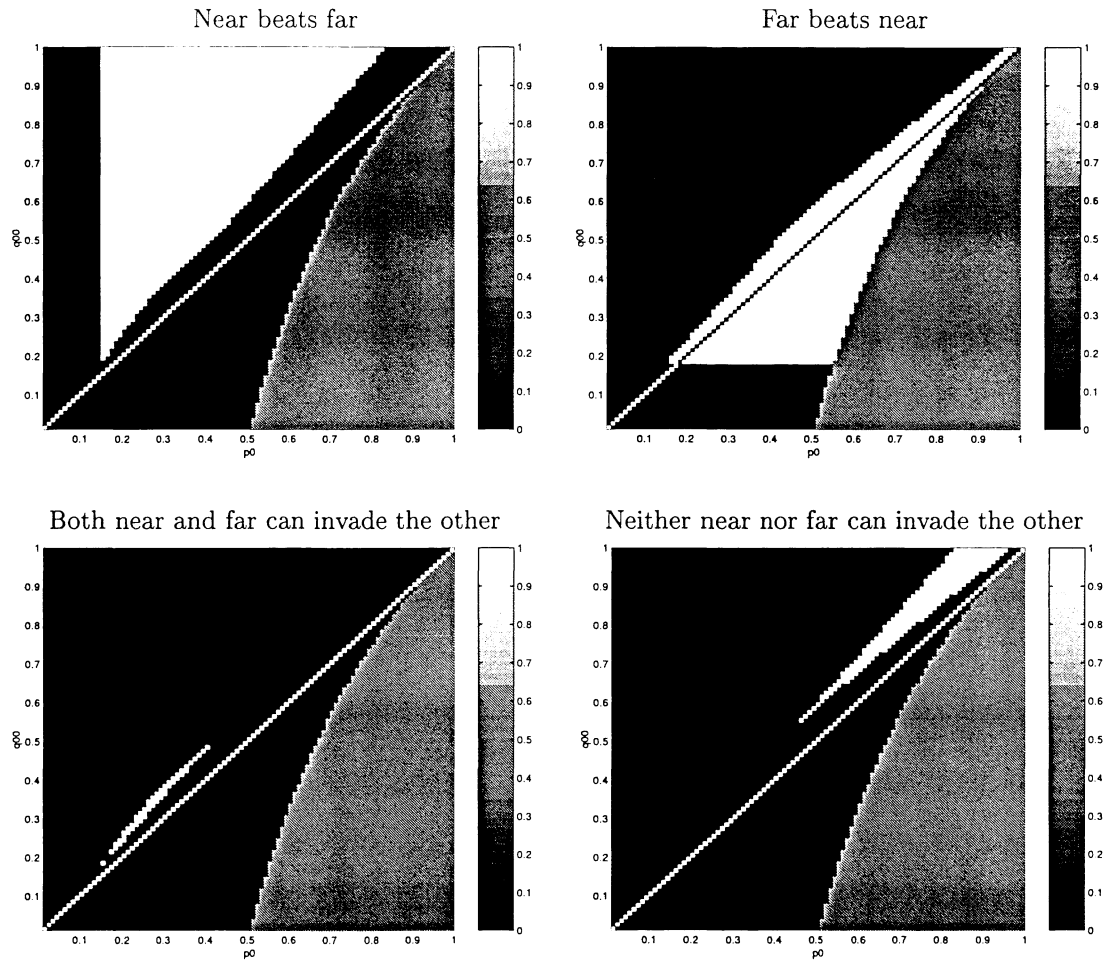

Figure 5: The four main outcomes of the invasion experiments, as predicted by pair approximations. See figure 2 for further explanation, and parameter values used. Also compare with figure 4.

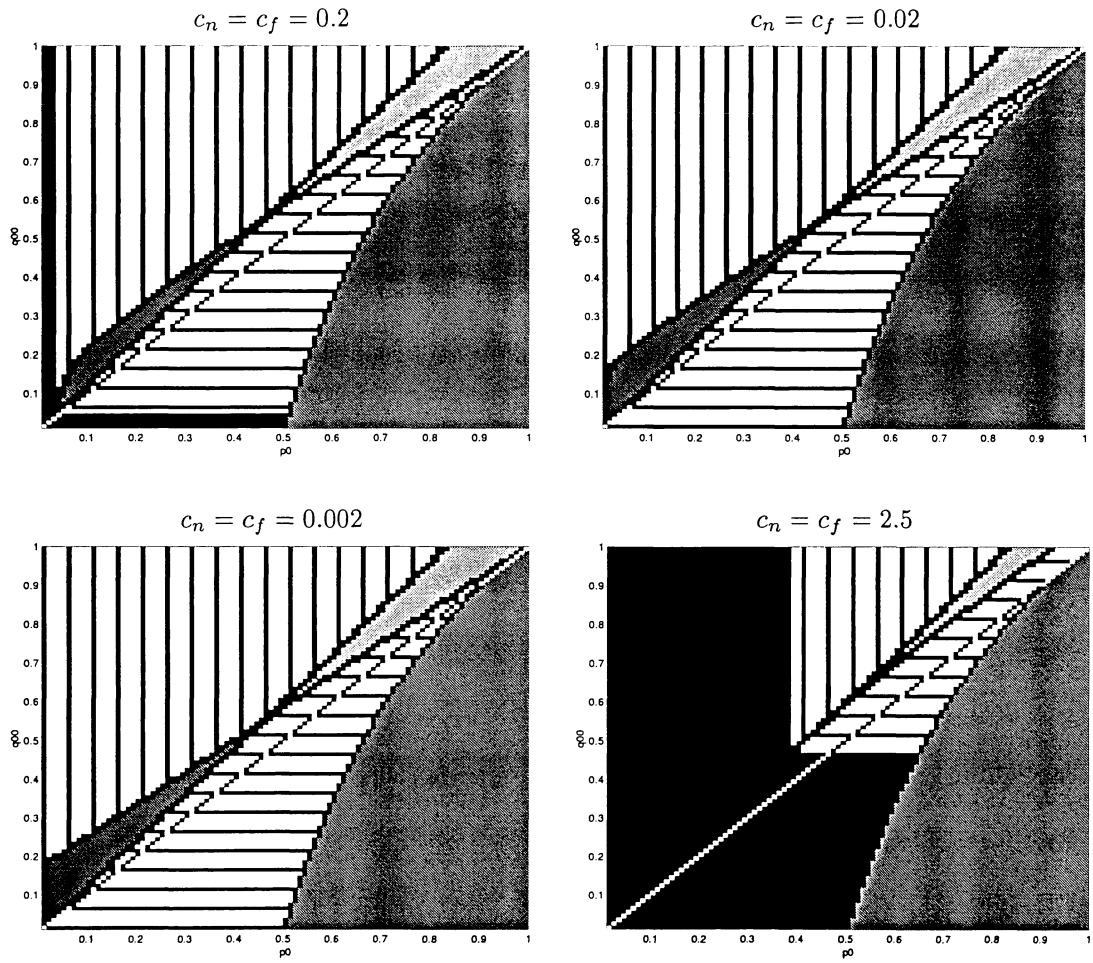

Figure 6: Predictions from pair approximations of the outcome of the model when the costs c_n and c_f are varied, i.e. fecundity is varied. The possible outcomes are: near beats far (vertical stripes), far beats near (horizontal stripes), each can invade the other (dark gray), and neither can invade the other (light gray). The black areas along the left and bottom edges, seen prominently in the lower right figure, are regions where one or both of the populations cannot survive even on their own.

If near and far dispersal have the same costs, the condition becomes $\mu > 0$, and pure far will always be able to invade pure near on such a landscape.

On the other hand, in order for near to invade far on a uniform landscape, equation (19) simplifies to

$$c_n < \frac{5c_f}{6}.$$

When $c_n = c_f$, this becomes $1 < 5/6$ which is obviously never satisfied.

In fact, it is only necessary to assume that $p_0 = q_{00}$ for this last result to be valid.

Result 4 *On landscapes with spatially uncorrelated heterogeneities, i.e. $p_0 = q_{00}$ (including the special case of uniform landscapes with 100% suitable habitat), pure near dispersal is able to invade pure far dispersal only if*

$$c_n < \frac{5c_f}{6}.$$

If both strategies have the same cost, near is never able to invade far.

Unfortunately, equation (7) cannot be simplified enough to determine if it is always true that far can invade near when $p_0 = q_{00}$, although the simulation and pair approximation results presented in figures 4, 5, and 6 seem to indicate that this is in fact true.

Finally, assuming $c_n = c_f$, consider a far-dispersing population on a landscape where $q_{00} < p_0$, i.e. there are negative correlations between habitat types of adjacent sites. On such landscapes, the probability that a neighbor of a suitable site is empty and suitable is $q_{00}(1 - s_f^*)$, while the probability that a randomly chosen site is empty and suitable is $p_0(1 - s_f^*)$, which is larger. Thus, a far-dispersing propagule will be more likely than a near-dispersing propagule to land on an empty suitable site. Thinking about the growth rate for a far disperser compared to that of an invader which is allocating any of its reproductive effort to near dispersal, near dispersal will be less successful than far dispersal, which gives:

Result 5 *When $q_{00} < p_0$ and the costs of near and far dispersal are equal, pure far dispersal will be an evolutionarily stable strategy, as no other strategy (including mixed strategies) will be able to invade.*

Finally, results from simulations and pair approximations for a mixed dispersal strategy consisting of 20% far and 80% near dispersal invading a pure near disperser are shown in figure 7. Clearly, pair approximations do a poor job for this situation, and fail to predict that the mixed dispersal strategy is able to successfully invade over a wide variety of landscape parameters. A modified version of the pair approximation was also tried, based on the idea of improved pair approximations (Sato et al., 1994), as follows. On the hexagonal lattice, a pair of adjacent sites have two neighbors in common. E.g. consider the pair of sites u and v in figure 8; they both have sites 2 and 6 as neighbors. In equation (30), the first term has a component $5Q[2|0]\phi_n$ describing the rate at which the empty site u receives propagules from its five neighbors labelled 1, 2, 6, 7, and 8 in figure 8, given that we know that site v is occupied. However, the probability that site 2 is occupied will be larger than $Q[2|0]$ if the population is clustered, since site 2 has another occupied neighbor. Another estimate of the probability that site is occupied is $Q[2|2]$, since site v is occupied and is also a neighbor of site 2. The same applies to site 6. With this in mind, the term $5Q[2|0]\phi_n$ in equation (30) was replaced with $3Q[2|0]\phi_n + 2Q[2|2]\phi_n$ and the results analyzed. However, there was no significant improvement in the predictions. Other variations of the pair approximation are possible on this lattice (van Baalen, 2000), but given the lack of improvement of the somewhat drastic variation mentioned above, as well as the striking inaccuracy of the pair approximation as compared to simulations, they are unlikely to offer much improvement.

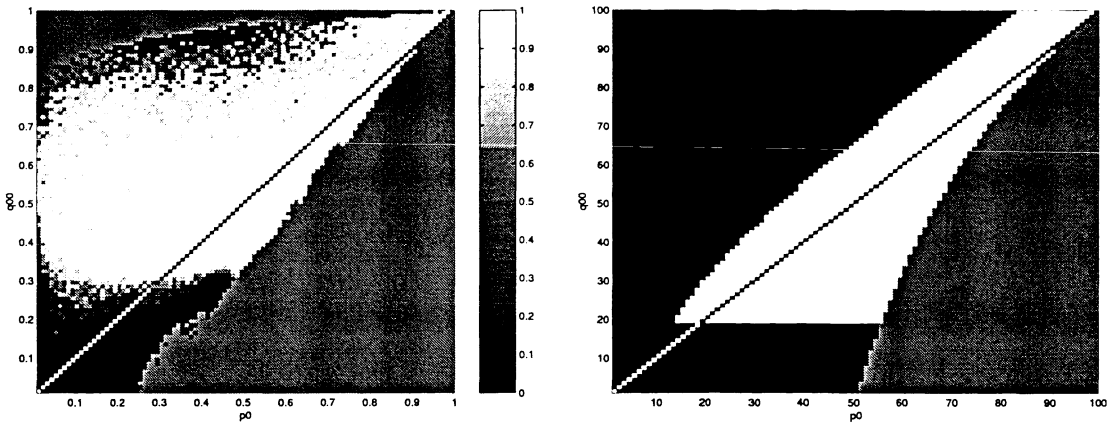

Figure 7: Results showing a mixed dispersal strategy consisting of 20% far dispersal and 80% near dispersal ($\alpha_2 = 0.2$) trying to invade a pure near disperser ($\alpha_1 = 0$). Left: results from simulations showing the proportion of times (out of 5 replicate simulations on independent landscapes) that the mixed strategy was able to invade the pure near disperser. Right: predictions from pair approximations. Axes are as in figure 2.

Discussion

The effects of an individual's reproductive efforts are affected both by interactions with other individuals (Ferrière and Le Galliard, 2001) as well as by the conditions of the region in which propagules land, or in general the distribution of "safe sites" (Green, 1983). This model investigates the ways in which fixed exogenous spatially correlated heterogeneities in habitat suitability, as well as the spatial distribution of a population, together create the distribution of safe and empty sites within which individuals must compete, and is another approach to studying competition-colonization tradeoffs (Bowers and Dooley, 1991; Dytham, 1995; Holmes and Wilson, 1998; Winkler and Fischer, 1999).

When pure near and pure far dispersal strategies interact, some of the results observed are not terribly surprising. On landscapes with high spatial correlations between habitat types of adjacent sites and little to medium global amounts of suitable habitat, near dispersal is superior. On such landscapes, near dispersal allows individuals to exploit contiguous patches of suitable sites, while far dispersal is a much more risky prospect due to the chances of landing on an unsuitable site. As the habitat becomes less clustered, far dispersal eventually becomes the superior strategy. Even when suitable habitat is somewhat clustered and would seemingly favor near dispersal because nearby sites are more likely to be suitable than distant sites, far dispersal is still superior, assuming the costs of near and far dispersal are equal. This is due to the fact that near dispersers themselves become aggregated, and waste many propagules by dropping them on sites which are already occupied; intraspecific competition and in fact competition between siblings or between individuals and their descendants then play a large role. The population itself transforms a landscape where suitable sites are clustered, into a landscape where safe sites (i.e. sites which are both suitable and empty) are more likely to be found far away from an occupied site. When both p_0 and q_{00} are large (but $q_{00} > p_0$, i.e. clustered habitat), whichever population is established first does well enough that the opposite dispersal strategy is unable to invade. Of course, if the relative costs of near or far dispersal were adjusted, one strategy may become superior on such landscapes.

These effects of habitat loss and fragmentation agree with those of Hiebeler (2000) and Ovaskainen et al. (2001). At first, they seem to contradict the results of Lavorel et al. (1994), who found that when two species with exponential dispersal distributions with different means interacted, the one with a shorter mean dispersal distance was competitively superior. They found these results on both aggregated and

disaggregated landscapes, in their terminology. However, all six of the landscapes used in their study in fact had $q_{00} > p_0$, and would thus be considered aggregated or clustered in terms of the parameters used here. It is therefore not surprising that they found shorter dispersal distances to be competitively superior on those clustered landscapes.

With pure dispersal strategies, the region of co-invasibility is generally quite small, as seen in figure 6. As fecundity increases, i.e. the costs c_n and c_f decrease, the region of co-invasibility does increase slightly.

On landscapes where there are no spatial correlations in habitat types, i.e. $p_0 = q_{00}$, it is never possible for near and far dispersal strategies to be coinvasible because near cannot invade far in that case. Thus in that situation it seems unlikely for those two strategies to be able to coexist. On uniform landscapes ($p_0 = q_{00} = 1$), far dispersal beats near dispersal, and the two strategies will not coexist.

This study did find that for certain spatial distributions of suitable habitat, however, coinvasibility and thus coexistence between near and far dispersers is possible. Note that for this case, for the near-dispersing population intraspecific competition is much stronger than interspecific competition, even at very low density, due to spatial aggregation of the near dispersers. Far dispersers by definition have no spatial aggregation, although at low density they will tend to compete with near dispersers more than their own kind under the random mixing behavior that they follow. For these particular types of habitat distribution, coexistence between the two strategies is facilitated by the patchy environment. The two species here differ in their dispersal strategy, although they utilize the same type of habitat. These results demonstrate that the effects of spatial structure on a species' ability to access resources is a kind of resource partitioning that can lead to stable coexistence, which touches on the topic of the ability for two identical species to coexist (Green, 1986; Chesson, 1991). It should be noted, however, that a bit of additional exploration with the models used here showed that for two truly identical species, i.e. with identical dispersal strategies, the species at low density could not invade, as its extinction equilibrium was neutrally stable.

When considering interactions between pure near and far strategies, pair approximations work quite well at predicting the various regions of invasibility, as seen by comparing figures 4 and 5. With pure strategies, pair approximations have the additional advantage that they can be completely solved analytically.

With mixed strategies, in some situations pair approximations do very poorly at predicting when one strategy can invade another, as can be seen in figure 7. This is somewhat surprising, since one might think that adding some degree of far dispersal to a pure near strategy should make the model behave more like the spatially implicit models, which can be predicted very accurately.

There are a couple of possible explanations for this. First, on some landscapes, there are often small patches of contiguous suitable sites which are surrounded by unsuitable habitat; these can be seen in the clustered landscape in the right part of figure 1. With a pure near disperser, these small patches of sites are prone to extinction due to their small size, and once they are empty, they cannot be recolonized by near dispersal. However, the pair approximation apparently does not recognize this phenomenon. If the limit as $\mu \to 0$ or $c_n \to 0$ is computed for the proportion of suitable sites occupied in equation (39), i.e. fecundity is increased greatly, the result is $s_n^* = 1$, all suitable sites are occupied. In fact however, in this situation, any small patches of suitable sites which were initially empty would remain empty, thus s_n^* should be less than one, depending on initial conditions.

Another explanation for the poor accuracy of the pair approximation for some interactions between populations with mixed dispersal is simply that various functions of the population density and clustering have very shallow slopes with respect to p_0 and q_{00}, and so a small error in these functions will shift the boundaries of regions of invasibility by a very large amount. Exploration of the invasibility criteria (stability of extinction equilibria) suggested that this was the case, at least for some of the invasion experiments used here.

Perhaps a version of improved pair approximations (Sato et al., 1994; van Baalen, 2000) other than the one tried here could more accurately predict the simulations. Or, since the equations for mixed dispersal already must be solved numerically, using larger blocks of sites to incorporate more information about spatial correlations would probably improve the predictions (Hiebeler, 1997). The number of states or terms in the equations involved would be large, but not nearly as large as in Hiebeler (1997), since the model here uses continuous time. Further investigation is needed to determine why the pair approximations used here fail

to predict the behavior of mixed dispersal strategies.

The simulation results in figure 7 indicate that, at least when competing against pure near dispersers, mixed dispersal changes the situation dramatically. Pure near dispersal will almost never be an evolutionarily stable strategy, as it can almost always be invaded by a mixed strategy. Simulation results from a strategy with 5% far dispersal invading pure near dispersal (not shown) indicated this even more strongly. Mixed dispersal strategies consisting of mostly near dispersal with occasional far dispersal reap many of the benefits of local dispersal, being able to take advantage of contiguous patches of suitable sites, while also having a mechanism for escaping the local population clustering that pure near dispersal creates. Likewise, when pure near tries to invade 20% far (also not shown here), it is only successful in a very small region of the landscape parameter space when p_0 is small and q_{00} is very large, i.e. highly clustered landscapes. Finally, recall that when $q_{00} < p_0$, i.e. on unclustered landscapes, far dispersal is an ESS.

Taken together, these results indicate that although the amount and distribution of habitat do play a crucial role in interactions between dispersal strategies, and thus the evolution of dispersal, intraspecific competition for space likely plays an even larger role. In this context at least, the answer to the question "does competition drive dispersal?" (Waser, 1985) is a resounding "yes," particularly on landscapes where there is a positive correlation between habitat types of nearby sites, which is probably the norm rather than the exception in nature.

The results also suggest that on clustered landscapes, an intermediate fraction of far dispersal, i.e. a mixed strategy, is likely to be the evolutionarily stable strategy. Unfortunately, the computational demands of the spatially explicit simulations prevent their use in fully exploring this issue, while standard pair approximations seem to break down much of the time when applied to mixed dispersal. Apparently, techniques somewhere slightly closer to the middle of this spectrum which ranges from spatially implicit models at one end to spatially explicit simulations at the other (Hiebeler, 1997), i.e. techniques with more information about spatial correlations than pair approximations can provide, will be necessary to further untangle questions about how competition for space affects the evolution of dispersal.

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Appendix A: Derivation of the Pair Approximations

Near dispersal

Because each site on the lattice may be in one of three states (0=empty, 1=unsuitable, 2=occupied), there are $3^2 = 9$ possible state configurations of a 2×1 block of sites. But symmetry assumptions, the fixed distribution of habitat types, and the constraint that probabilities must sum to one reduces the number of equations to three (Hiebeler, 2000). The equations for the near disperser are very similar to those developed in Hiebeler (2000), but in continuous time and on a hexagonal lattice.

For the near disperser, as explained in the text, the total rate of propagule production for an occupied site is R_T/c_n. Since each propagule is dropped on one of the six neighboring sites chosen at random, the rate at which an occupied site colonizes any particular one of its neighbors is $\phi_n = R_T/(6c_n)$. Thus, the pair approximation equations are

$$\frac{dP[00]}{dt} = 2P[02]\mu - P[00](10\gamma\phi_n) \tag{20}$$

$$\frac{dP[01]}{dt} = P[21]\mu - P[01](5\gamma\phi_n) \tag{21}$$

$$\frac{dP[02]}{dt} = P[00](5\gamma\phi_n) + P[22]\mu - P[02](5\gamma\phi_n + \phi_n + \mu) \tag{22}$$

where $\gamma = P[02]/P[0]$ is the conditional probability that a randomly-chosen neighbor of an empty suitable site is occupied.

To derive equation (20), observe that the only way to gain a block of empty suitable sites, i.e. a [00] block, is for the occupied site in either a [02] or a [20] block to become empty. The occupied site in a [02] block becomes empty at rate μ, and since $P[02] = P[20]$, we obtain the $2P[02]\mu$ term. Next, the only way to lose a [00] block is for either one of the sites to be colonized. Figure 8 shows the pair of sites we are considering, drawn in bold and labelled u and v, along with their eight neighbors, labelled 1–8. There are ten edges between the uv pair and their neighbors. The rate of propagules coming across any particular edge from one of the neighbors is γ, the probability that the neighbor is occupied, times ϕ_n, the rate of propagules from an occupied site to its neighbor. Thus the total rate of propagules coming into the pair of sites uv, i.e. the rate at which we lose a [00] block due to colonization by neighboring sites, is $10\gamma\phi_n$.

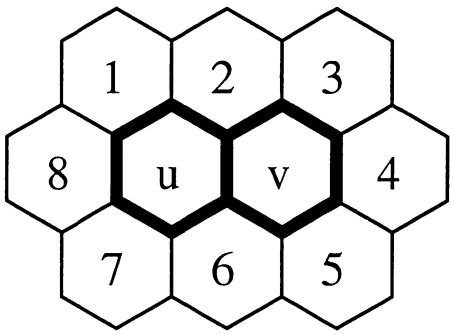

Figure 8: A pair of adjacent sites, labelled u and v, along with their eight neighbors.

Similar reasoning can be used to derive the other two equations. For example, the most complicated term is the third term in equation (22), describing the rate at which [02] blocks are lost. Consider figure (8) again, where site u is in state 0 and site v is in state 2. There are three ways to lose a [02] block: first, the occupied site v may become empty, which happens at rate μ. Next, the empty site u may be colonized by the adjacent occupied site v, which happens at rate ϕ_n. Finally, the empty site u may be colonized by one of its five other neighbors, each of which has probability γ of being occupied, so the total rate of colonization from these five neighbors is $5\gamma\phi_n$.

Next, using the identities

$$P[12] = p_0(1 - q_{00}) - P[01] \quad (23)$$

$$P[22] = p_0 q_{00} - P[00] - 2P[02], \quad (24)$$

from Hiebeler (2000), equations (20)–(22) can be rewritten in the form given in equations (1)–(3).

Far dispersal

For the far disperser, because no spatial correlations develop in the population, it would be possible to accurately describe the system using only spatially implicit equations (sometimes referred to as mean field equations), i.e. equations describing the state frequencies for single sites, rather than pairs of sites. That information, along with the landscape parameters p_0 and q_{00} would make it possible to then compute the 2×1 block probabilities $P[ij]$. However, for consistency with the near dispersal model, pair approximations will be used here as well.

With far dispersal, the total rate of propagule production for each occupied site is $\phi_f = R_T/c_f$. Occupied sites (i.e. sites in state 2) send their propagules to other sites chosen at random uniformly across the entire

lattice. Thus if there are N sites on the landscape, and proportion $P[2]$ of them are occupied, the total rate of propagule production is $NP[2]\phi_f$. But since the probability that a propagule lands on a particular site is $1/N$, the total rate of propagules landing on a particular site is simply $P[2]\phi_f$.

The pair approximation equations for the far disperser are thus

$$\begin{aligned}
\frac{dP[00]}{dt} &= 2P[02]\mu - P[00](2P[2]\phi_f) \\
\frac{dP[01]}{dt} &= P[21]\mu - P[01](P[2]\phi_f) \\
\frac{dP[02]}{dt} &= P[22]\mu + P[00](P[2]\phi_f) - P[02](P[2]\phi_f + \mu).
\end{aligned}$$

Consider for example the second term in the first equation. In order to lose a [00] block, one of the two sites must be colonized. The rate of propagules landing on any single site is $P[2]\phi_f$. Since either site in the [00] block may be colonized, the total rate of colonization to the block is $2P[2]\phi_f$.

Using equations (23) and (24) again, the three equations above can be rewritten as equations (9)–(11).

Mixed dispersal

With mixed dispersal, the pair approximation equations are essentially a combination of those for near and far dispersal, since propagules may arrive at empty sites via near dispersal from adjacent sites, or via far dispersal from anywhere on the lattice. Thus, the equations are merely combinations of those for near and far dispersal:

$$\begin{aligned}
\frac{dP[00]}{dt} &= 2P[02]\mu - 2P[00](5\phi_n Q[2|0] + \phi_f P[2]) \\
\frac{dP[01]}{dt} &= P[21]\mu - P[01](5\phi_n Q[2|0] + \phi_f P[2]) \\
\frac{dP[02]}{dt} &= P[22]\mu + P[00](5\phi_n Q[2|0] + \phi_f P[2]) - P[02](\mu + \phi_n + 5\phi_n Q[2|0] + \phi_f P[2])
\end{aligned}$$

where $Q[i|j] = P[ij]/P[j]$ is the conditional probability that a randomly chosen neighbor of a site in state j is in state i.

Using equations (23) and (24), and letting $\beta = 5\phi_n Q[2|0] + \phi_f P[2]$ be the rate of propagules arriving at an empty site via near dispersal from five neighbors and via far dispersal, the equations above may be rewritten in the form given in equations (15)–(17).

Appendix B: Stability of extinction equilibrium

Here I analyze the stability of the extinction equilibrium for the pair approximation models, i.e. the state where the population size has reached zero. For all three dispersal models (near, far, and mixed), when the population size reaches zero, the 2×1 block probabilities are: $P^*_E[00] = p_0 q_{00}$, $P^*_E[01] = p_0(1 - q_{00})$, and $P^*_E[02] = 0$. The first two probabilities, derived in Hiebeler (2000) are simply determined by the landscape parameters p_0 and q_{00}. The third probability is zero, since no sites are occupied (i.e. in state 2). Thus the extinction equilibrium is:

$$\vec{E} = \begin{bmatrix} P^*_E[00] \\ P^*_E[01] \\ P^*_E[02] \end{bmatrix} = \begin{bmatrix} p_0 q_{00} \\ p_0(1 - q_{00}) \\ 0 \end{bmatrix}.$$

Near dispersal

For the near dispersal model, the Jacobian matrix for equations (1)–(3) evaluated at the extinction equilibrium is

$$J|_{\vec{E}} = \begin{bmatrix} 0 & 0 & 2\mu - 10\phi_n q_{00} \\ 0 & -\mu & -5\phi_n(1-q_{00}) \\ -\mu & 0 & 5\phi_n q_{00} - \phi_n - 3\mu \end{bmatrix}$$

which gives the characteristic equation

$$\left|J|_{\vec{E}} - \lambda I\right| = -(\mu+\lambda)\left[(-\lambda)(5\phi_n q_{00} - \phi_n - 3\mu - \lambda) + \mu(2\mu - 10\phi_n q_{00})\right] = 0$$

One obvious root is $\hat{\lambda} = -\mu$, which when factored out leaves only a quadratic equation in λ. In order for the extinction equilibrium to be unstable, i.e. in order for the population to persist, we need at least one of the other roots $\hat{\lambda}$ of the characteristic equation to have positive real part. This happens precisely when

$$\mu < 5\phi_n q_{00}. \tag{25}$$

As long as equation (25) is satisfied, the pair approximation predicts that the near-dispersing population will not go extinct.

Far dispersal

A similar analysis of the far dispersal model given by equations (9)–(11) yields the characteristic equation

$$\left|J|_{\vec{E}} - \lambda I\right| = -\lambda^3 + \lambda^2(p_0\phi_f - 4\mu) + \lambda(3\mu p_0\phi_f - 5\mu^2) + 2p_0\phi_f\mu^2 - 2\mu^3 = 0.$$

The three roots are $\hat{\lambda}_1 = -\mu$, $\hat{\lambda}_2 = -2\mu$, and $\hat{\lambda} = p_0\phi_f - \mu$. Thus, the extinction equilibrium will be unstable and the far-dispersing population will not go extinct if the third root is positive, i.e.

$$\mu < p_0\phi_f \tag{26}$$

Mixed dispersal

The roots of the characteristic equation for the mixed-dispersal model cannot be put into a simple analytic form for testing. However, an alternative approach to analyzing stability of the extinction equilibrium with pair approximations is a technique described in Matsuda et al. (1992). This technique recognizes that a population at low density, i.e. with $P[2]$ small, quickly becomes clustered (assuming near dispersal), or in general the degree of clustering reaches an equilibrium very quickly relative to the time scale over which $P[2]$ is changing. In other words, local clustering probabilities such as $Q[2|2]$ converge to an equilibrium value very quickly relative to $P[2]$, so one first solves for the equilibrium Q probabilities, and then uses them to determine whether or not $P[2]$ grows.

It is possible to write down a set of differential equations for the conditional probabilities $Q[0|2]$ and $Q[2|2]$, as follows. First, the model must be reformulated using a different parameterization. Rather than using $P[00], P[01]$, and $P[02]$, we can use $P[2]$, $P[02]$, and $P[22]$. In terms of these state variables, the mixed-dispersal model becomes

$$\frac{dP[2]}{dt} = -\mu P[2] + P[2]\left(\phi_f(p_0 - P[2]) + 6\phi_n Q[0|2]\right) \tag{27}$$

$$\frac{dP[22]}{dt} = -2\mu P[22] + 2P[02]\left(P[2]\phi_f + \phi_n + 5Q[2|0]\phi_n\right) \tag{28}$$

$$\frac{dP[02]}{dt} = -P[02]\left(\mu + \phi_n + 5Q[2|0]\phi_n + P[2]\phi_f\right) + P[22]\mu + \tag{29}$$

$$P[00]\left(\phi_f P[2] + 5Q[2|0]\phi_n\right) \tag{30}$$

To write down a differential equation for $Q[0|2]$, we simply use the definition $Q[0|2] = P[20]/P[2] = P[02]/P[2]$, and use the quotient rule:

$$\frac{dQ[0|2]}{dt} = \frac{d}{dt}\left(\frac{P[02]}{P[2]}\right) = \frac{\frac{dP[02]}{dt}}{P[2]} - \frac{P[02]}{P[2]} \cdot \frac{\frac{dP[2]}{dt}}{P[2]}.$$

Substituting equations (27) and (30) into the relation above, taking the limit as $P[2] \to 0$, and simplifying gives

$$\frac{dQ[0|2]}{dt} = Q[0|2]\left((5q_{00} - 1)\phi_n - \phi_f p_0 - 6\phi_n Q[0|2]\right) + Q[2|2]\mu + p_0 q_{00}\phi_f. \tag{31}$$

Applying a similar trick to $Q[2|2] = P[22]/P[2]$ yields

$$\frac{dQ[2|2]}{dt} = 2Q[0|2]\phi_n - Q[2|2]\left(\mu + \phi_f p_0 + 6\phi_n Q[0|2]\right). \tag{32}$$

Once the equilibrium values $Q^*[0|2]$ and $Q^*[2|2]$ from equations (31) and (32) are found, $Q^*[0|2]$ may then be plugged back into equation (27) and the stability of the equilibrium $P^*[2] = 0$ analyzed. Near $P^*[2] = 0$, equation (27) behaves like the simple exponential growth equation

$$\frac{dP[2]}{dt} = P[2](\phi_f p_0 + 6\phi_n Q^*[0|2] - \mu)$$

Thus, as long as $\phi_f p_0 + 6\phi_n Q^*[0|2] - \mu > 0$, then $P[2]$ will grow, i.e. the extinction equilibrium is unstable.

Unfortunately, the needed equilibrium Q values for equations (31) and (32) also cannot be solved for in a concise analytical form, but they can easily be obtained numerically. For this study, the standard fourth-order Runge-Kutta method was used to integrate the equations to find their equilibrium.

Note that this technique of letting the Q's first relax to their equilibrium and then determining the stability of $P[2]$ yields exactly the same results for this model as numerically solving for the eigenvalues of the Jacobian matrix.

Appendix C: Non-trivial equilibria

Near dispersal

The system of equations (1)–(3) have a non-trivial equilibrium under certain conditions. We wish to solve for s^*, the proportion of suitable sites which are occupied at equilibrium. First, since the proportion of all sites $P[2]$ which are suitable and occupied satisfies $P[2] = p_0 - P[0] = p_0 - (P[00] + P[01] + P[02])$, then

$$\frac{dP[2]}{dt} = -\frac{dP[00]}{dt} - \frac{dP[01]}{dt} - \frac{dP[02]}{dt}. \tag{33}$$

Substituting equations (1)–(3) into the equation above and simplifying yields

$$\frac{dP[2]}{dt} = 6P[02]\phi_n - P[2]\mu. \tag{34}$$

At equilibrium, $dP[2]/dt = 0$, which implies

$$P^*[02] = P^*[2]\mu/(6\phi_n). \tag{35}$$

Substituting this into equation (4), we have

$$\gamma^* = \frac{P^*[02]}{P^*[0]} = \frac{P^*[2]\mu}{6\phi_n(p_0 - P^*[2])}.$$

Substituting the expressions for $P^*[02]$ and γ^* above into equation (1) and setting $dP[00]/dt = 0$, we can solve for

$$P^*[00] = \frac{(p_0 - P^*[2])\mu}{5\phi_n}. \tag{36}$$

Doing the same thing with equation (2) and setting $dP[01]/dt = 0$ gives

$$P^*[01] = \frac{6p_0(1-q_{00})(p_0 - P^*[2])}{6p_0 - P^*[2]}. \tag{37}$$

Substituting equations (35)–(37) into the relation $s^* = P^*[2]/p_0 = 1 - (P^*[00] - P^*[01] - P^*[02])/p_0$ gives

$$s^* = 1 - \frac{\mu(1-s^*)}{5\phi_n} - \frac{6(1-q_{00})(1-s^*)}{6-s^*} - \frac{s^*\mu}{6\phi_n}$$

This can be rewritten as a quadratic equation

$$g(s^*) = (s^*)^2(30\phi_n - \mu) + (s^*)(-30\phi_n + 12\mu - 180\phi_n q_{00}) + (180\phi_n q_{00} - 36\mu) = 0. \tag{38}$$

Analysis of this quadratic equation shows that as long as inequality (25) is satisfied, i.e. the extinction equilibrium is unstable, then the parabola described by equation (38) will be concave up, and also $g(0) > 0$ and $g(1) < 0$, which together imply there is a single root s^* satisfying $0 \le s^* \le 1$. This root, the smaller of the two roots of this quadratic, is the nontrivial equilibrium value of s^*, the proportion of sites occupied. (The larger root is greater than 1, and thus is not biologically meaningful.) The nontrivial equilibrium is thus:

$$s^* = \frac{15\phi_n + 90\phi_n q_{00} - 6\mu - 15\sqrt{\phi_n}\sqrt{\phi_n(6q_{00}-1)^2 + 4\mu(1-q_{00})}}{30\phi_n - \mu}. \tag{39}$$

Far dispersal

The same ideas can be applied to far dispersal, with much simpler results. Equation (33) can also be applied to the far-dispersing population. When equations (9)–(11) are substituted in, the result is:

$$\begin{aligned} \frac{dP[2]}{dt} &= -\frac{dP[00]}{dt} - \frac{dP[01]}{dt} - \frac{dP[02]}{dt} \\ &= P[2](\phi_f(p_0 - P[2]) - \mu) \end{aligned}$$

Note that unlike equation (34), this equation is self-contained, i.e. it does not depend on $P[00]$, $P[01]$, or $P[02]$. This is because of the lack of spatial correlations in the far-dispersing population. Using $s = P[2]/p_0$, we have $ds/dt = s(\phi_f p_0(1-s) - \mu)$. Setting $ds/dt = 0$ at equilibrium, either $s^* = 0$ (trivial equilibrium), or

$$s^* = 1 - \frac{\mu}{p_0\phi_f} \tag{40}$$

Note that this equilibrium satisfies $0 \le s^* \le 1$, i.e. it is biologically meaningful, precisely when inequality (26) is satisfied, i.e. when the extinction equilibrium is unstable.

Mixed dispersal

The non-trivial equilibrium for the mixed dispersal model cannot be solved for analytically. When it was needed for the invasibility experiments, the differential equations were numerically integrated using the standard fourth-order Runge-Kutta method, until the system reached equilibrium.